

BIOLOGY AND TAXONOMY OF SPECIES OF *OPHIOPSYLLUS* AND *PSEUDANTHESSIUS* (COPEPODA) ASSOCIATED WITH BRITTLE STARS (OPHIUROIDEA) IN BELIZE

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ABSTRACT

Three copepod associates are reported from shallow-water ophiuroids at Belize, Central America. Two are cancerillid siphonostomatoids: *Ophiopsyllus latus*, new species, and *Ophiopsyllus reductus*. The third is a pseudanthessiid poecilostomatoid, *Pseudanthessius deficiens*. The last species, previously known from *Ophioderma cinereum*, was also found on *Ophioderma brevispinum*. In contrast, species of *Ophiopsyllus* appear to be host-specific. *Ophiopsyllus reductus* is found exclusively on *Ophiocoma echinata*. *Ophiopsyllus latus* is found only on *Ophiocomella ophiactoides* (with the exception of two doubtful records from *Ophiocoma pumila*). Previous records of *Ophiopsyllus reductus* on *Ophiocomella ophiactoides* are incorrect. Comparisons between Jamaican and Belizean populations of *Ophiopsyllus latus* reveal similarities and differences and suggest that the parasitic effects of the species are minimal. On approximately 17–57% of *O. ophiactoides* examined there are 1–4 *O. latus*, which generally clasp the first or second arm joint near the edge of the disk. They face toward the mouth of the host, possibly orienting to the currents emanating from the bursae or to food in the oral region. In Belize, only one instance of physical injury to the host was noted, although parasitic damage has been reported in Jamaica. Furthermore, a published report that *O. latus* inhibits the sexual reproduction of the host appears to be unwarranted.

This report, dealing with several species of copepods that are associated with Belizean ophiuroids, is based on quantitative collections made primarily during 1981 and 1982, supplemented with more recently collected material. After the conclusion of our initial field studies (which are described in Hendler and Littman, 1986; Hendler and Peck, 1988), two accounts appeared of the association between a cancerillid copepod and its ophiuroid host (Emson et al., 1985; Emson and Mladenov, 1987), which seemed to render our observations redundant. Upon reexamination of those reports and of our specimens and notes, it became evident that the copepods that we and Emson et al. had collected represent an undescribed, previously misidentified species. In the light of our findings we are able to provide a description of the new species, *Ophiopsyllus latus*, and novel biological information on it and on its only congener, *Ophiopsyllus reductus* Stock, Humes, and Gooding, 1963. In addition, we supplement the previously published information on *Pseudanthessius deficiens* Stock, Humes, and Gooding, 1963, a copepod associated with ophiodermatid ophiuroids.

MATERIALS AND METHODS

Each of the three copepod species was sampled differently. Specimens of *O. latus*, new species, were found on ophiuroids collected and processed as described by Hendler and Littman (1986) and Hendler and Peck (1988). Data on the species are based on a series of specimens collected on 6 April 1980 and 22–26 April 1981, except where noted below. Thirteen small, brooding and fissiparous ophiuroid species, from among the 44 ophiuroid species found on the Belize barrier reef, were systematically examined for symbionts using a stereomicroscope. The brittle stars were generally

extracted from the alga *Halimeda opuntia* (Linnaeus) Lamouroux, a refuge substrate (sensu Hendler and Littman, 1986). Specimens of the other, larger species, found among corals and rubble, were examined for associates only sporadically. The ophiuroids were studied after anesthetization and preservation to find the number and position of copepods on each specimen.

Specimens of *O. reductus* were gathered during a survey of the ophiuroids on the reef flat and the spur and groove zone seaward of Carrie Bow Cay, Belize (sites described in Hendler and Littman, 1986). The various ophiuroid species accumulated from corals and coral rubble were placed together in large plastic bottles underwater. In the laboratory the different species were separated, anesthetized with magnesium sulfate crystals, and preserved in separate containers.

Pseudanthessius deficiens was found in Hidden Creek, a mangrove channel at Twin Cays, in the Belize barrier reef lagoon (16°49.8'N, 88°5.9'W). At that locality, specimens of *Ophioderma brevispinum* (Say, 1825) were placed individually in plastic bags that were sealed under water. Formalin was added to each bag in the laboratory to preserve ophiuroid commensals, and the ophiuroids were measured and transferred with their symbionts to ethanol.

The collection of *P. deficiens* may accurately reflect the copepod population on the hosts, based on the manner in which individual hosts were treated. Due to the methods used to collect the two species of *Ophiopsyllus*, individuals may have been displaced or lost while the ophiuroids were collected and processed.

The three species of copepods were removed from the hosts and preserved in ethanol. Measurements and drawings are based on specimens in lactic acid. The measurements of the total length of the body do not include the setae on the caudal rami. The segments of the antennule were measured along their posterior margins. All figures were drawn with the aid of a camera lucida. All copepods were collected by G. Hendler.

TAXONOMY AND BIOLOGY

Siphonostomatoida Thorell 1859

Cancerillidae Giesbrecht 1897

Ophiopsyllus Stock, Humes, and Gooding 1963

Ophiopsyllus latus new species

(Figs. 1–3)

Type Material.—6 females, 2 males, from *Ophiocomella ophiactoides* (H. L. Clark. 1901), in 0–2 m, Carrie Bow Cay, Belize, Central America, 16°48.1'N, 88°04.8'W, sta. 20, 22 April 1981. Holotype female (USNM 243638), allotype male (USNM 243639), and six paratypes (5 females, 1 male) (USNM 243640) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Other Specimens (all from *Ophiocomella ophiactoides* at Carrie Bow Cay, Belize).—Deposited in the National Museum of Natural History, Smithsonian Institution, Washington: 5 females, 2 males (USNM 243641), in 0–2 m, 16°48.1'N, 88°04.8'W, sta. 22, 22 April 1981; 2 females, 1 male (USNM 243642), in 9.1 m, 16°48.2'N, 88°04.6'W, sta. 23, 23 April 1981. Deposited in the Natural History Museum of Los Angeles County, Los Angeles, California: 2 females, 1 male (LACM 81–229.2), in 0–2 m, 16°48.12'N, 88°04.8'W, sta. 43, 26 April 1981; 2 females, 1 male (LACM 81–257.2), in 1–2 m, 16°48.1'N, 88°04.73'W, sta. 41, 25 April 1981; 2 females (LACM 81–257.1), in 1–2 m, 16°48.1'N, 88°04.8'W, sta. 41, 25 April 1981). Remaining specimens in the collection of AGH: 1 female, in 9.1 m, 16°48.2'N, 88°04.6'W, sta. 24, 23 April 1981; 1 female, 2 males, in 1–2 m, 16°48.1'N, 88°04.8'W, sta. 46, 26 April 1981; 1 male, in 15.2 m, 16°48.2'N, 88°04.6'W, sta. 42, 6 April 1980; 2 females, in 0–2 m, 16°48.1'N, 88°04.8'W, sta. 19, 22 April 1981; 1 female, in 0–2 m, 16°48.1'N, 88°04.8'W, sta. 21, 22 April 1981; 1 male, in 9.1 m, 16°48.1'N, 88°04.6'W, sta. 35, 24 April 1981; 1 male, in 0–2 m, 16°48.1'N, 88°04.8'W, sta. 21, 22 April 1981; 1 male, in 1–2 m, 16°48.1'N, 88°04.8'W, sta. 53, 26 April 1981.

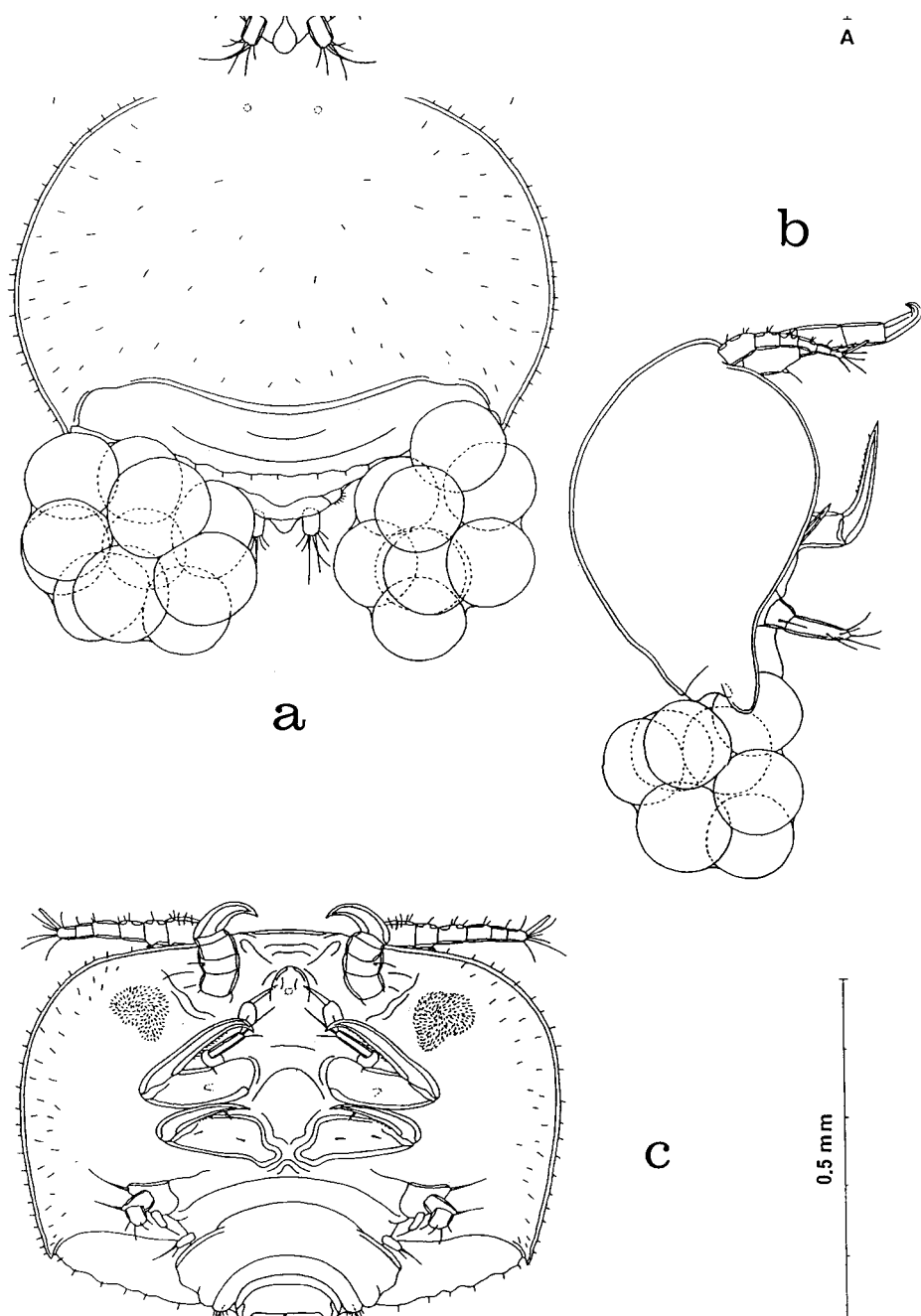


Figure 1. *Ophiopsyllus latus* new species, female. a, body, dorsal (scale A); b, body, lateral, surficial ornamentation not shown (A); c, body ventral (A).

*Additional Specimens (all in the collection of AGH).—*From juvenile *Ophiocoma pumila*?: 1 female (LACM 83–323.1), in 9 m, at Carrie Bow Cay, Belize, 16°48.2'N, 88°04.6'W, 16 January 1983; from mixed ophiuroids including *O. pumila*, 2 females (LACM 85–458.2), in 0.2–1.5 m, 16°48.12'N, 88°04.73'W, CBC 85–14, 21 June 1985. From *O. ophiactoides*: 1 male, in 1–5 m, western side of Loggerhead Key, Dry Tortugas, Florida, 29 September 1982.

Female.—Body (Fig. 1A–C) in dorsal view with broad cephalosome, sides rounded, concealing appendages except antennules. Length 0.60 mm (0.58–0.63 mm) and greatest width 0.76 mm (0.72–0.79 mm), based on 4 specimens. Greatest dorsoventral thickness 0.36 mm. Cephalosome moderately inflated (Fig. 1B), with length to width ratio 0.74:1. Ratio of length to width of body 0.79:1. Posterior corners of cephalosome pointed in dorsal and ventral views (Fig. 1A,C), but more rounded in lateral view (Fig. 1B). Posterior border of cephalosome less sclerotized than elsewhere and slightly scalloped.

Urosome (Fig. 2B) in dorsal view partly concealed under cephalosome (Fig. 1A), but in 1 female urosome bent anteroventrally and entirely hidden (Fig. 2A), except tips of setae on caudal rami. Somite bearing leg 5 fused with genital somite, forming composite somite (genital complex; see Kabata, 1979) $120 \times 265 \mu\text{m}$, ratio 0.45:1, laterally indented posteriorly. Genital areas located dorsolaterally at broadest part of somite. Two postgenital somites, first somite short, $29 \times 125 \mu\text{m}$, and partly concealed under posterior edge of composite genital somite, second somite (anal somite) longer, $68 \times 122 \mu\text{m}$, having posteromedian rounded hyaline flange between caudal rami.

Caudal ramus (Fig. 2C) unornamented, $57 \times 81 \mu\text{m}$, ratio of length to width 1.84:1. Six setae, from outer to inner $55 \mu\text{m}$ (inserted somewhat on dorsal surface of ramus), 37, 30, 86, 30, and $40 \mu\text{m}$ (this last seta apparently representing dorsal seta, here moved to insert on edge of ramus). All setae smooth.

Rostral area weak (Fig. 2D).

Antennule (Fig. 2E,F) 6-segmented, $290 \mu\text{m}$ long. Lengths of segments 81 (116 μm along anterior margin), 34, 41, 38, 34, and $29 \mu\text{m}$, respectively. Formula for armature: 6, 1, 4, 2, 1, and $6 + 1$ aesthetasc. First and second segments with distal row of several setules on posterior border. Antenna (Fig. 3A) 4-segmented, length $300 \mu\text{m}$, including large terminal claw. Exopod on second segment (Fig. 3B) $6 \times 6 \mu\text{m}$, seta $21 \mu\text{m}$. Coxa, basis, and first segment of endopod without setae or ornamentation. Second segment of endopod (bearing terminal claw) having 3 setae and minute knob (Fig. 3C) and bearing few outer setules (Fig. 3A). Claw recurved, stout, $112 \mu\text{m}$ long (Fig. 3A,C,D), showing minute refractile points on antero-inner surface (Fig. 3C).

Siphon (Fig. 2D) bluntly rounded at tip. Mandible (Fig. 3E) with stout basal part bearing slender stylet $83 \mu\text{m}$, with diagonal tip bearing row of minute spinules. Maxillule (Fig. 3F) 2-segmented. First segment broad, unarmed. Second segment elongated, bearing 5 distal setae and 1 small proximal seta. Maxilla (Fig. 3G) 2-segmented. First segment unarmed. Clawlike second segment $180 \mu\text{m}$ long, with recurved tip, ornamented with inner spinules and having small inner subterminal spine. Maxilliped (Fig. 3H) 2-segmented. First segment with 2 setae, 1 proximal on inner margin, 1 distal. Second clawlike segment showing incomplete division at distal one-fourth, having recurved tip with subterminal seta, proximally with 1 setule and 2 small blunt processes and inner row of small spinules.

Ventral postoral area as in Fig. 1C. No postoral protuberance.

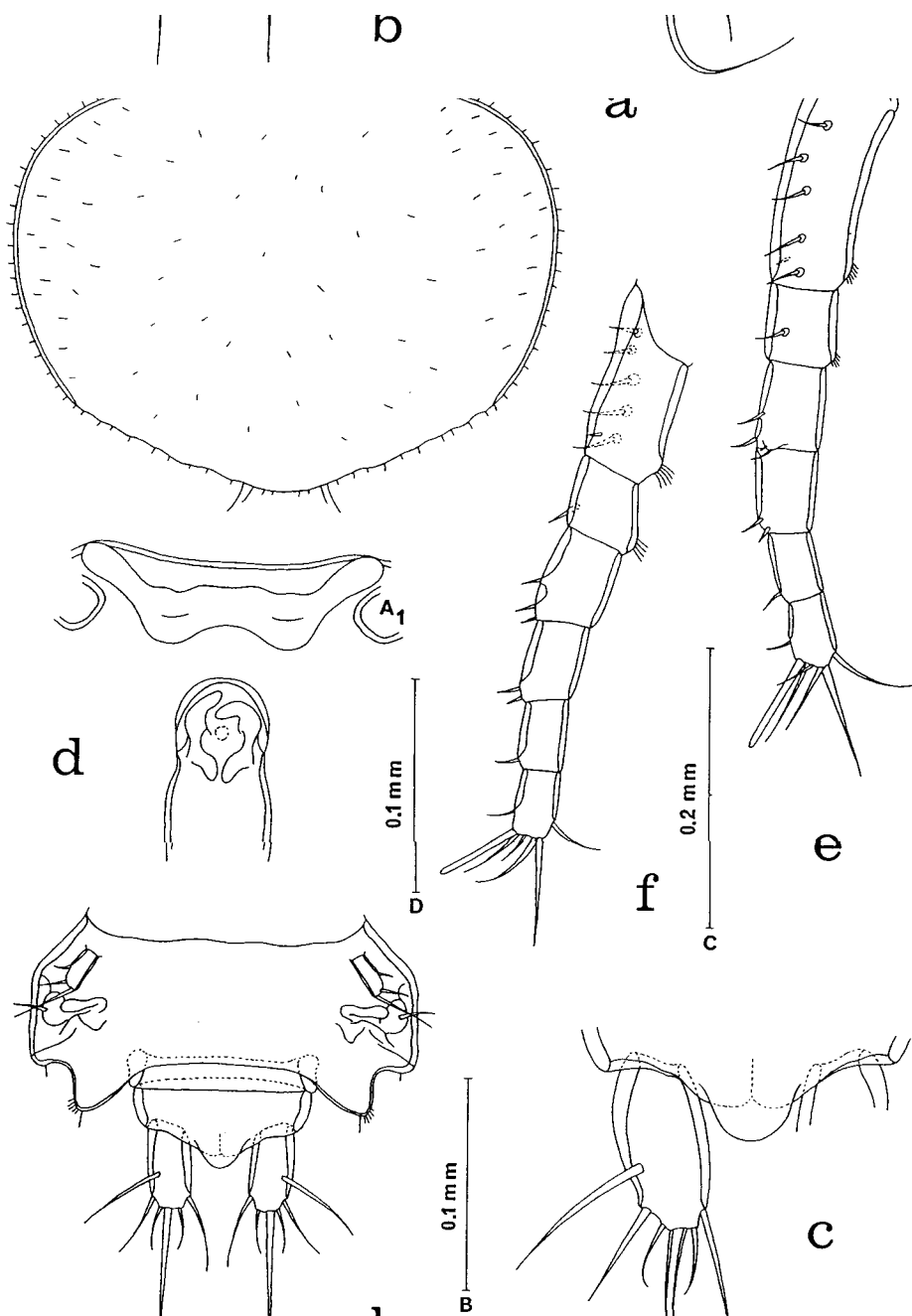


Figure 2. *Ophiopsyllus latus* new species, female. a, body, dorsal, with urosome concealed beneath (scale A); b, urosome, dorsal (B); c, caudal ramus, dorsal (C); d, rostral area and siphon, ventral (D); e, antennule, ventral (D); f, antennule, dorsal (D). A1 = position of antennule.

Leg 1 (Fig. 3I) with unarmed coxa, basis with outer seta. Exopod 1-segmented, carrying 6 setae, from outer to inner 50, 19, 25, 22, 23, and 12 μm . Endopod 1-segmented, small, with 2 terminal setae 14 μm . All setae smooth. Leg 2 (Fig. 3j) single elongate segment $34 \times 11 \mu\text{m}$, bearing smooth terminal seta 44 μm . Legs 3 and 4 absent.

Leg 5 (Fig. 2B) single small segment $23 \times 10 \mu\text{m}$ on dorsal side of composite genital somite bearing 3 setae.

Leg 6 (Fig. 2B) represented by 1 seta 21 μm long.

Egg sac (Fig. 1a,b) approximately $374 \times 297 \mu\text{m}$, containing 8–11 eggs, with an average number of 9, ranging in diameter from 125–156 μm .

Cephalosome with many small setules (sensilla?) on dorsal and lateral surfaces, continuing on part of ventral surface (Fig. 1A,C). Patch of minute spinules on ventral surface lateral to base of antenna (Fig. 1C). Urosome and caudal rami without ornamentation, except row of few setules (one longer than others) on posterolateral corner of genital somite (Fig. 2B). Pair of small internal round sclerotized bodies near rostral region visible (Fig. 1A) in specimens cleared in lactic acid.

Color of living ovigerous specimens: cephalosome with opaque white pattern, eggs brown or purplish brown.

Male.—Body (Fig. 3K) smaller than female, $0.40 \times 0.42 \text{ mm}$, wider than long, ratio 0.95:1. Ratio of length to width of cephalosome 0.8:1.

Appendages similar to those of female.

Composite genital somite (Fig. 3L) $78 \times 166 \mu\text{m}$, much wider than long, ratio 0.47:1, with leg 5 located on dorsal side as in female.

Spermatophore (Fig. 3M), attached to genital somite of female, sausage-shaped, $109 \times 62 \mu\text{m}$.

Ornamentation of body similar to that of female.

Color of living male not recorded.

Etymology.—The species name, *latus*, Latin, meaning broad, refers to the broad cephalosome as seen in dorsal view.

Remarks.—*O. latus* differs from its only congener, *O. reductus* Stock, Humes, and Gooding, 1963, in several ways. In *O. reductus* (1) the length of the body is 0.68 mm (0.61–0.78 mm) and the width is 0.60 mm (0.51–0.66 mm), longer than wide, the ratio being 1.13:1 (measurements from original description); (2) the cephalosome is laterally indented; (3) the egg sac contains 3–7 eggs (2 or 3 in original description), with an average of 4; (4) refractile internal bodies lateral to insertions of the antennae seen in specimens cleared in lactic acid; (5) the anal somite protrudes only slightly between the caudal rami; (6) the antenna has a dense covering of small spinules; (7) the dorsal surface of the cephalosome has many long setules; (8) an area of prominent spinules occurs on the ventrolateral surface of the cephalosome lateral to the antennae; (9) the urosome and caudal rami have many long surficial setules; and (10) the host is *Ophiocoma echinata*.

In general body form, *Ophiopsyllus* resembles two other monotypic cancerillid genera. *Ophiopsyllopsis indicus* Sebastian, 1968, lives in the genital bursa of the brittle star *Ophiactis* sp. on the southeastern coast of India. Based on its original description, *Ophiopsyllopsis* differs, however, from *Ophiopsyllus* in several ways: (1) the 4-segmented antennule, (2) the absence of an exopod on the antenna, and (3) leg 5 represented by a peglike projection bearing 1 spine and 1 seta. *Parophiopsyllus ligatus* Humes and Hendler, 1972, is associated with the ophiuroid *Amphioplus abditus* (Verrill) in Connecticut and with *Amphioplus sepultus* Hendler, 1985 (as *Amphioplus* sp.) in Florida (Humes and

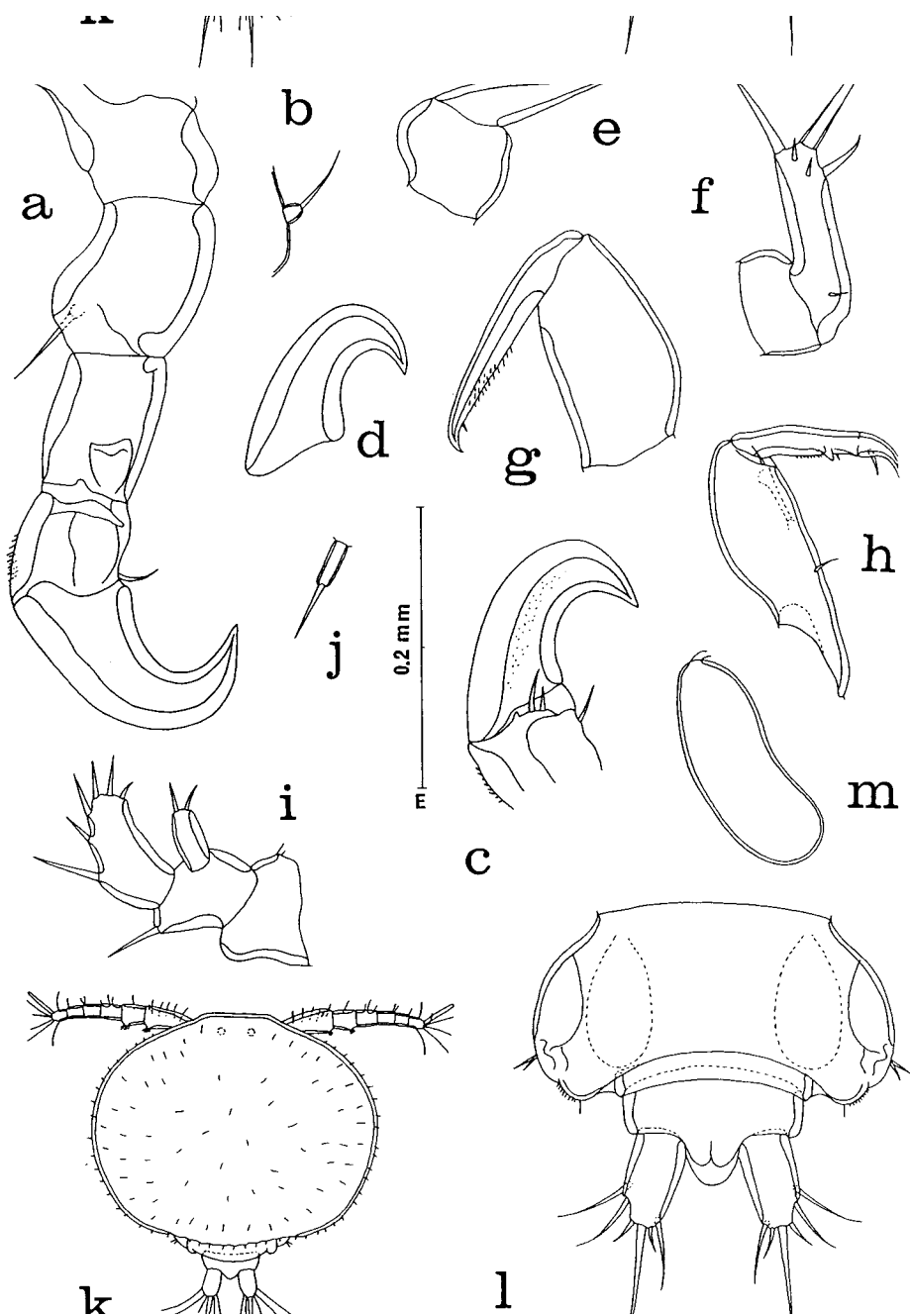


Figure 3. *Ophiopsyllus latus* new species. Female. a, antenna (scale D); b, exopod of antenna, inner (C); c, claw of antenna, postero-inner (D); d, claw of antenna, antero-outer (D); e, mandible, ventral (C); f, maxillule, ventral (C); g, maxilla, ventral (E); h, maxilliped, ventral (E); i, leg 1, ventral (C); j, leg 2, ventral (E). Male. k, body, dorsal (A); l, urosome, ventral (B); m, spermatophore, attached to female, ventral (D).

Hendler, 1972; see Hendler, 1995, for the distinction between *A. abditus* and *A. sepultus*). *Parophiopsyllus* differs from *Ophiopsyllus* chiefly in the following features: (1) a 5-segmented antennule and (2) the absence of leg 5.

Thirteen small, fissiparous or brooding ophiuroid species were examined microscopically for the presence of associated copepods; 31 larger species were examined less thoroughly (see species lists in Hendler and Littman, 1986; Hendler and Peck, 1988). With two possible exceptions, *O. latus* occurred only on *O. ophiactoides* (H. L. Clark, 1901). On 16 January 1983, a female was found on a juvenile *O. pumila* Lütken, 1859, from among a large collection of algae in which *O. ophiactoides* also occurred. It is possible that this specimen of *O. latus* may have dislodged and shifted hosts, or that the host was incorrectly identified. Two males were found in a sample of various ophiuroids, including *O. pumila*, collected on 21 June 1985.

Ophiocomella ophiactoides is extremely similar in appearance to juvenile *O. pumila* Lütken, 1859, although several characteristics help to distinguish it (Hendler et al., 1995). One of the most notable distinguishing features is its ability to reproduce asexually by splitting the disk in two, and like most fissiparous ophiuroids it generally has six arms of which three are usually longer and three are shorter and newly regenerating.

Ophiopsyllus latus was found at depths from 0–15 m in habitats spanning the backreef to the forereef dropoff. It occurred predominately on ophiuroids living in the calcareous alga *H. opuntia*, and rarely on hosts in corals (23 vs 4 host individuals). While this discrepancy mirrors the relative abundance of *O. ophiactoides* in different reef substrates (see Hendler and Littman, 1986), it is not necessarily a reflection of active habitat selection by the copepods. In addition, most hosts bearing *O. latus* occurred on the reef crest ($n = 20$). Fewer *O. ophiactoides* with copepods were found on the shallower, protected reef flat ($n = 4$), or the deeper spur and groove zone ($n = 3$) and the forereef dropoff ($n = 1$). These figures for the incidence of symbiosis parallel the abundance of the host species in different reef zones (see Hendler and Littman, 1986; Hendler and Peck, 1988), and may not reflect the preference of the copepod in different areas of the reef.

As noted in the "Materials and Methods", copepods were undoubtedly lost during collection, preservation, and sorting. Thus, it is possible that the figures for their abundance and sex ratios are inaccurate. *Ophiopsyllus latus* appeared to be moderately common, and affected hosts were not heavily infested. It was seen on 29 of the 164 individuals of *O. ophiactoides* that were examined (17.7% occurrence). The hosts harbored from 1–4 associates (mean = 1.8, SD = 0.47, $n = 29$); 14 ophiuroids had a single copepod, and lesser numbers (8 ophiuroids) had two copepods, three copepods (5 ophiuroids), or four copepods (2 ophiuroids). Many of the ophiuroids lacked female copepods carrying egg sacs, but others had one copepod (10 ophiuroids), two copepods (6 ophiuroids), or three females with eggs (2 ophiuroids). The number of female copepods ($n = 30$) exceeded the number of males ($n = 13$). Eleven hosts bore only female copepods, 5 had only males, and 6 had copepods of both sexes.

Most of the copepods were oriented facing toward the center of the disk of the ophiuroid and clasping the host's second arm joint. None were found distal to the fourth joint. Twenty-nine copepods were found on joint 2, six between 2 and 3, seven on 3, one between 3 and 4, and two on joint 4. However, some specimens collected from 1983 and 1985 had copepods beneath the disk, on the first arm joint. Five copepods were on the disks of the ophiuroids, and of those on the arms of the host, 12 had the cephalosome in contact with the disk and another eight were in contact with the bursal slit. There were

about as many ($n = 17$) on the small, regenerating arms of the ophiuroids as there were ($n = 23$) on longer arms, indicating that the copepods shift position or recruit to hosts without prejudice for the length of the arm they occupy ($P > 0.05$, Chi-square test). When living animals were examined, one of the *O. ophiactoides* was incidentally noted to have tissue damage that was apparently caused by a copepod. In that instance, the copepod was affixed to the central dorsal surface of the host's disk. Fifteen preserved ophiuroids with 31 *O. latus*, each host with 1–5 associates were examined, using a stereomicroscope, for evidence of damage caused by the copepods. Their disks were not ruptured or deformed, the arm spines were intact, and the arm plates were not deformed. Nevertheless, more subtle abrasion of the integument would have been detectable only using electron microscopic examination.

Ophiopsyllus reductus Stock, Humes, and Gooding, 1963
(Fig. 4)

Material Examined.—(all from *O. echinata* (Lamarck) at Carrie Bow Cay, Belize). Deposited in the Natural History Museum of Los Angeles County, Los Angeles, California: 10 females, 2 males (LACM 80–176.1), in 3.0–6.1 m, 16°48.2'N, 88°04.6'W, sta. 25, 31 March 1980; 10 females, 5 males (LACM 80–177.1), in 0–2 m, 16°48.1'N, 88°04.8'W, sta. 29, 1 April 1980. In the collection of AGH: 1 female, in 3.0–9.1 m, 16°48.1'N, 88°04.6'W, sta. 37, 4 April 1980.

Female.—Body (Fig. 4A) with cephalosome more slender than in *O. latus*, with sides slightly indented. Length 0.68 mm (0.62–0.73 mm) and width 0.59 mm (0.54–0.63 mm), based on 10 specimens. Ratio of length to width of body 1.16:1. Ratio of length to width of cephalosome 0.77:1. Posterior corners of cephalosome rounded in dorsal view.

Medial hyaline flange on anal somite between caudal rami only slightly extended posteriorly (Fig. 4A).

Cephalosome dorsally and laterally with many setules, ventrally with patch of prominent stout spinules (Fig. 4B), each approximately 7 μ m long.

Siphon extended anteriorly (Fig. 4A), reaching slightly beyond anterior rim of cephalosome.

Urosome ornamented as in Figure 4A.

Egg sac with 3–7 eggs (Fig. 4C–F), eggs approximately 130–140 μ m in diameter.

Male.—Body (Fig. 4G) resembling that of female but smaller. Length 0.58 mm (0.54–0.62 mm) and width 0.46 mm (0.44–0.52 mm), based on 5 specimens. Ratio of length to width of cephalosome 0.94:1. Ratio of length of body to greatest width 1.26:1.

Remarks.—*Ophiopsyllus reductus* was originally reported on *O. echinata* from Curaçao (see Stock et al., 1963a) and is described in the present report from the same species of ophiuroid in Belize. As explained in the discussion below, previous reports (Emson et al., 1985; Emson and Mladenov, 1987) that *O. reductus* occurs on *O. ophiactoides* appear to be incorrect.

The individuals described herein were collected from one ophiuroid on the reef flat (depth 0–2 m) which carried 5 male and 10 female copepods. Six ophiuroids from the spur and groove zone (depth 3–9 m) each bore 1–4 copepods. There were three male and 10 female copepods in all, and copepods of both sexes were found together on two ophiuroids.

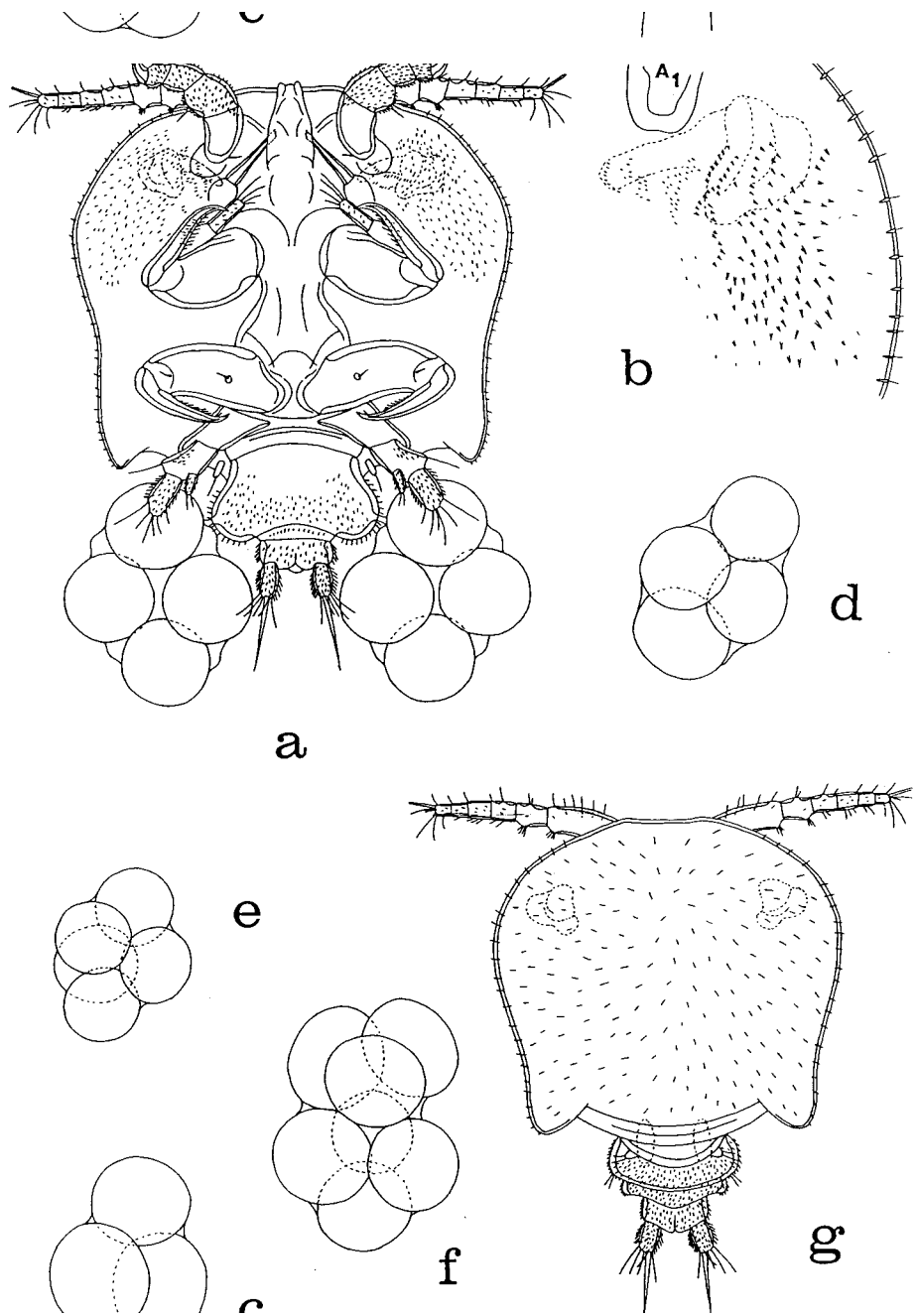


Figure 4. *Ophiopsyllus reductus* Stock, Humes, and Gooding, 1963. Female. a, body, ventral (scale A); b, patch of spinules lateral to mouthparts and posterior to insertion of antennule, ventral (E); c, egg sac, ventral (A); d, egg sac, ventral (A); e, egg sac, ventral (A); f, egg sac, ventral (A). Male. g, body, dorsal (A). A1 = position of antennule.

Poecilostomatoida Thorell, 1859

Pseudanthessiidae Humes and Stock, 1972

Pseudanthessius Claus, 1889

Pseudanthessius deficiens Stock, Humes, and Gooding, 1963

Material Examined.—Deposited in the Natural History Museum of Los Angeles County, Los Angeles, California: 4 females, 5 males, and 1 copepodid (LACM 82–135.1), from *Ophioderma brevispinum* (Say), in 1–2 m, Hidden Creek Mangrove Channel, Twin Cays, Belize, 16°49.8'N, 88°05.9'W, sta. 3, 6 June 1982; 3 females, 1 copepodid, from *Ophioderma cinereum*, in 1–2 m, same locality, CBC 89–31, (LACM 89–426.1), 12 March 1989.

Remarks.—*Pseudanthessius deficiens* has been reported previously from the ophiuroid *Ophioderma cinereum* Müller and Troschel, 1842, in Curaçao, St. Martin, and Puerto Rico (Stock et al., 1963b). The few specimens from the holothurian *Holothuria* (*Ludwigothuria*) *mexicana* Ludwig, 1875, in Curaçao are probably the result of sample contamination (Stock et al., 1963b: 56).

Most of our specimens were associated with *Ophioderma brevispinum* which were collected from a mangrove cay in the Belize barrier reef lagoon. *Ophioderma cinereum*, from which *P. deficiens* was first reported, also lives in Belize, where it occurs in close proximity to *O. brevispinum* (see Hendler et al., 1995). On 12 March 1989, 3 individuals of *O. cinereum* at our study site were examined for the presence of associates and 4 *P. deficiens* were recovered.

On 6 June 1982, 11 specimens of *P. deficiens* were found on *O. brevispinum* (see Material Examined), the males outnumbering females 6 to 4. Two males, 3 females, and a copepodid were found individually on 6 ophiuroids, 2 males on another individual, and 1 female and 2 males on a third individual. In a collection made on 3 June 1983, copepods were found on 5 of 7 *O. brevispinum*, and on 21 March 1983, there were copepods on 11 of 29 ophiuroids collected.

The egg sacs were broken in all of the ovigerous females collected by Stock et al. (1963b). We can now confirm that in *P. deficiens* the egg sacs are elongated, measuring $286 \times 132 \mu\text{m}$ in one female, and $292 \times 157 \mu\text{m}$ in another, and contain many eggs $47\text{--}52 \mu\text{m}$ in diameter. In a living ovigerous female there was a white pattern on the cephalosome and the eggs were white as well.

DISCUSSION

Copepods of several families are associated with ophiuroids on the eastern coast of North America and in the Caribbean. Among the copepods living externally, the pseudanthessiid *Pseudanthessius deficiens* Stock, Humes, and Gooding, 1963, is found with *Ophioderma cinereum* Müller and Troschel, 1842 (Stock et al., 1963b). The cancerillid *Ophiopsyllus reductus* Stock, Humes, and Gooding, 1963, occurs on *O. echinata* (Lamarck, 1816) (Stock et al., 1963a). The cancerillid *Parophiopsyllus ligatus* Humes and Hendler, 1972, and the clausiid (synaptophilid; see Ho, 1984) *Presynaptiphilus amphiopli* Humes and Hendler, 1972, are associated with *Amphioplus abditus* (Verrill, 1871) and *Amphioplus sepultus* Hendler, 1995 (see Humes and Hendler, 1995). Several species of *Cancerilla* cling to the arms of the “cosmopolitan species” *Amphipholis squamata* (Della Chiaje, 1828) (see Hendler et al., 1995), and one, *C. durbanensis* Stephensen, 1933, can induce a

growth anomaly in the host (Mortensen, 1933). In addition, three new asterocherid copepods from brittle stars in Jamaica, Puerto Rico, and Barbados are currently being described (Humes, in press).

Internal parasites of ophiuroids include *Critomolgus astrophyticus* (Humes and Stock, 1973), a parasitic lichomolgid that lives in the stomach of the basket star *Astrophyton muricatum* (Lamarck, 1816) (Humes and Stock, 1973). A parasitic thespesiopsyllid was reported in the stomach of *Ophiactis lymani* Ljungman, 1871, and in *Ophiactis savignyi* (Müller and Troschel, 1842) (Boffi, 1972). An unnamed internal parasite in of *A. squamata* from Rhode Island, U.S.A., initially regarded as a species of *Philichthys* Hérouard, 1906, has been most recently placed in the genus *Parachordeumium* Le Calvez, 1938 (Boxshall, 1988). Individuals parasitic in *A. squamata* from Connecticut, U. S. A., were described by Goudey-Perrière (1979) as *Amphiuophilus* (= *Parachordeumium*) *hendleri* and *A. humesi*. Other copepods endoparasitic in ophiuroids have been reviewed by Boxshall (1988).

The biology of these copepods and the nature of their association with ophiuroids is little known, with the exception of a few species. Some aspects of the population dynamics of *Pseudanthessius ligatus* and *amphiopli* associated with *Amphioplus* spp. have been described (Humes and Hendler, 1972), and the castrating relationship between *Parachordeumium amphiurae* and *A. squamata* has been investigated (Emson et al., 1988; Whitfield and Emson, 1988). Additional studies (Emson et al., 1985; Emson and Mladenov, 1987) concern the morphology, growth, distribution, behavior, and also the possible parasitic effects of putative *O. reductus* on *O. ophiactoides*. However, in those studies *O. latus* was incorrectly identified as *O. reductus*. Moreover, their description of damage inflicted on the host seems exceptional for an external copepod associate. Our observations suggest that the parasitic effects of the species is minimal.

The copepod studied by Emson et al. differs markedly from the description and drawings of authentic specimens of *O. reductus* (Stock, Humes, and Gooding, 1963a; this paper). However, the precise correspondence of the scanning electron microscope photographs of "*O. reductus*" in Emson et al. (1985), with the illustrations of *O. latus*, new species, in the present paper, indicate that they are both the same. Emson et al. (1985: 170) wrote that their specimens "may not be *O. reductus* but a very similar species of the same genus, specifically associated only with *O. ophiactoides*". Our specimens, however, conform closely to the description of Stock et al. (1963). "Their speculation that "localized populations have become specifically associated with different species [of ophiuroids] in different locations" appears to be incorrect.

Both species in the genus *Ophiopsyllus* occur on confamilial ophiuroids and seem to be host-specific throughout their overlapping geographic ranges. Our results show that *O. reductus*, which was first found on *O. echinata* in Curaçao, is associated with the same host species in Belize. Moreover, *O. latus*, described in the present report from specimens associated with *O. ophiactoides* from Belize and from the Dry Tortugas, Florida, was collected from the same host species in Jamaica (Emson et al., 1985) and in Belize (Emson and Mladenov, 1987).

Emson and Mladenov (1987) found that the incidence of association between *O. latus* and *O. ophiactoides* was 56.8% in Jamaica and 23% in Belize, the latter figure in fairly close agreement with the 17% incidence that we report for Belize. The mean number of copepods per host (<2) which Emson and Mladenov (1987) reported for Jamaica approximates our finding for Belize, but in the present study the proportion of male to female copepods was markedly lower than that reported for Jamaica.

Emson and Mladenov (1987) found *O. latus* on only *O. ophiactoides* among the seven species of ophiuroids that they examined, and, with two possible exceptions, we found it on only one of 44 ophiuroid species in Belize. Thus their experimental finding that the copepod will readily associate with ophiuroids other than *O. ophiactoides* may be an artifact of experimental procedure rather than a reflection of the typical behavior of this species.

Our observations on the behavior of the copepods on *O. ophiactoides* corroborate some of the findings of Emson et al. (1985). We too noted that the maxilla (= second maxilla) appear to be used to clasp the host. Although the preferred attachment site of these copepods varies somewhat, it is clear that the copepods generally cling to the host's second and third arm joints and do not venture distad to the fourth. The proximity between copepod cephalosome and ophiuroid disk, and particularly the bursa of the ophiuroids, which was noted in the present study, suggests that *O. latus* may orient to the respiratory currents generated within the bursae of the host. However, it is also possible that the copepods are attracted to food, which accumulates near the region of the mouth of the ophiuroid.

In most cases, the nature of the associations between copepods and their ophiuroid hosts is not known. Therefore, the suggestion of parasitism by *O. latus* on *O. ophiactoides* is noteworthy (Emson et al., 1985: 160). Emson et al. indicated that the copepod caused tissue discoloration and damage and the loss of arm spines in "heavily parasitized" hosts. Although they found that the mean number of copepods per ophiuroid host was less than 2, just as we did in Belize, they did not explicitly report the frequency of "heavy parasitization". Therefore, the extent and degree of parasite-induced tissue damage among the Jamaican ophiuroid population is unknown. In Belize, possible tissue damage was noted incidentally in only one of the 28 living parasitized *O. ophiactoides* examined, and no evidence of tissue damage or spine loss was found in an additional 15 preserved parasitized specimens. Could differences in the Jamaican and Belizean material indicate that the interaction between copepods and ophiuroids varies geographically?

In addition, Emson et al. (1985) reported an elevated incidence of *O. latus* on individuals of *O. ophiactoides* with six fully regenerated arms. Since newly divided, fissiparous ophiuroids have arms of unequal length, they speculated that the copepods repress sexual reproduction in the host. However, they also found that the percentage of infesta. and the number of associated *O. latus* vary directly with the size of *O. ophiactoides*. In effect, they suggested that large individuals of *O. ophiactoides* had divided less frequently than small individuals. However, the reproductive pattern for *O. ophiactoides* is not different from that of other fissiparous species that lack associated copepods. In these species, the larger, older ophiuroids also tend to have six equally long arms, presumably because they have ceased to reproduce asexually (Lütken, 1872). Clearly, cessation of fission need not involve the suppression of reproduction by copepods. In *O. ophiactoides* there may simply be more copepods on large non-dividing individuals because larger, older hosts provide a more extensive and stable attachment surface for commensals. Unfortunately, exactly what causes fissiparous ophiuroids to stop dividing and to grow to a large size has not yet been experimentally determined (A. M. Clark, 1967). Further research is required in that arena, and additional observations are needed to accurately gauge the physiological effects of *O. latus* on *O. ophiactoides*.

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LITERATURE CITED

- Boffi, E. 1972. Ecological aspects of ophiuroids from the phytal of S.W. Atlantic Ocean warm waters. *Mar. Biol.* 15: 316–328.
- Boxshall, G. A. 1988. A review of the copepod endoparasites of brittle stars (Ophiuroidea) *Bull. Brit. Mus. Nat. Hist. (Zool.)* 54: 261–270.
- Clark, A. M. 1967. Variable symmetry in fissiparous Asterozoa. *Symp. Zool. Soc. London* 20: 143–157.
- Emson, R. H. and P. V. Mladenov. 1987. Brittlestar host specificity and apparent host discrimination by the parasitic copepod *Ophiopsyllus reductus*. *Parasitology* 94: 7–15.
- _____, P. Whitfield, and P. Blake. 1988. The influence of parasitization on the population dynamics of *Amphipholis squamata*. Pages 737–744 in R. D. Burke, P. V. Mladenov, P. Lambert, and R. L. Parsley, eds., *Echinoderm Biology. Proc. 6th Int'l. Echinoderm Conf.* Balkema, Rotterdam, The Netherlands. P. xiii, 1–818.
- _____, P. V. Mladenov, and I. C. Wilkie. 1985. Studies of the biology of the West Indian copepod *Ophiopsyllus reductus* (Siphonostomatoida: Cancerillidae) parasitic upon the brittlestar *Ophiocomella ophiactoides*. *J. Nat. Hist.* 19: 151–171.
- Goudey-Perrière, F. 1979. *Amphiurophilus amphiurae* (Hérourard). Crustacé Copépode parasite des bourses génitales de l'ophiure *Amphipholis squamata* Della Chiaje, Echinoderme: morphologie des adultes et étude des stades juvéniles. *Cah. Biol. Mar.* 20: 201–230.
- Hendler, G. 1995. New species of brittle stars from the Western Atlantic, *Ophionereis vittata*, *Amphioplus sepultus*, and *Ophiostigma siva*, and the designation of a neotype for *Ophiostigma isocanthum* (Say) (Echinodermata: Ophiuroidea). *Contrib. Sci., Nat. Hist. Mus. Los Angeles Co.* 458: 1–19.
- _____, and B. S. Littman. 1986. The ploys of sex: relationships among the mode reproduction, body size and habitats of coral-reef brittlestars. *Coral Reefs* 5: 31–42.
- _____, and R. W. Peck. 1988. Ophiuroids off the deep end: Fauna of the Belizean fore-reef slope. Pages 411–419. in R. D. Burke, P. V. Mladenov, P. Lambert, and R. L. Parsley, *Echinoderm biology. Proc. 6th Int'l. Echinoderm Conf.* Balkema, Rotterdam, The Netherlands. P. xiii, 1–818.
- _____, J. E. Miller, D. L. Pawson, and P. M. Kier. 1995. Sea stars, sea urchins, and allies. *Echinoderms of Florida and the Caribbean*. Smithsonian Inst. Press, Washington and London. P. i–xi, 1–390.
- Hérourard, E. 1906. Sur un nouveau copépode parasite d'*Amphiura squamata*. *C. R. Hebd. Séance. Acad. Sci. Paris* 142: 1287–1289.
- Ho, J.-S. 1984. New family of poecilostomatoid copepods (Spiophanicolidae) parasitic on polychaetes from southern California, with a phylogenetic analysis of nereicoliform families. *J. Crust. Biol.* 4: 134–146.
- Humes, A. G. In press. Copepoda (Siphonostomatoida) associated with Ophiuroidea in Jamaica, Puerto Rico, and Barbados. *Zool. Verh. Leiden*.
- _____, and G. Hendler. 1972. New cyclopoid copepods associated with the ophiuroid genus *Amphioplus* on the eastern coast of the United States. *Trans. Amer. Micr. Soc.* 91: 539–555.

- _____ and J. H. Stock. 1973. A revision of the family Lichomolgidae Kossmann, 1878, cyclopoid copepods mainly associated with marine invertebrates. *Smithson. Contrib. Zool.* 127: i-v, 1-368.
- Kabata, Z. 1979. Parasitic Copepoda of British fishes. The Ray Society, London, England. 152: 1-468.
- Lütken, C. F. 1872. Ophiuridarum novarum vel minus cognitarum descriptiones nonnullae. Beskrivelser af nogle nye eller mindre bekjendte Slangestjerner. Övers. K. Danske Vidensk. Selsk. Skr. Forh. 2(1872): 75-158.
- Mortensen, T. 1933. Echinoderms of South Africa. (Asteroidea and Ophiuroidea). *Vidensk. Meddr. Dansk Naturh. Foren. København* 93: 215-400.
- Sebastian, M. J. 1968. On a new genus and species of cancerillid copepod *Ophiopsyllopsis indicus*. *Zool. Anz.* 180: 68-75.
- Stock, J. H., A. G. Humes and R. U. Gooding. 1963a. Copepods associated with West Indian invertebrates - II Cancerillidae, Micropontiidae (Siphonostoma). *Stud. Fauna Curaçao* 15: 3-23.
- _____, _____ and _____. 1963b. Copepods associated with West Indian invertebrates - IV The genera *Octopicola*, *Pseudanthessius* and *Meomicola* (Cyclopoida, Lichomolgidae). *Stud. Fauna Curaçao* 18: 1-74.
- Whitfield, P. J. and R. H. Emson. 1988. *Parachordeumium amphiuræ*: A cuckoo copepod? *Hydrobiologia* 167/168: 523-531.

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